

Phagism Relationships among Butterflies

FRANK SLANSKY JR.¹

DEPARTMENT OF ENTOMOLOGY, CORNELL UNIVERSITY, ITHACA, N. Y. 14850

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Abstract: Relationships of major families of Nearctic butterflies (Papilionidae, Pieridae, Lycaenidae, and Nymphalidae) to the taxa and growth-forms of their larval food-plants are investigated and compared to those of the Palearctic butterflies. The Palearctic butterfly fauna consists of more than three times as many species as the Nearctic fauna and yet the relative percentages of species in each of the families are strikingly similar. In terms of the butterflies in the four major families as a group, the greatest percentage of species in the Nearctic are monophagous with approximately equal percentages of oligophagous and polyphagous species; the greatest percentage in the Palearctic are oligophagous followed by a fairly high percentage of polyphagous species and a lower percentage of monophagous species. High percentages of herb- and of shrub-feeders and lower percentages of tree-feeders are found in both regions. A higher percentage of species are specialized (monophagous and oligophagous) than are generalized (polyphagous) on each plant growth-form (herbs, shrubs, and trees) in both regions, a seemingly unexpected finding based upon current theories of plant-herbivore interactions.

Although the distinctions between phagism categories are arbitrary, physiological differences exist in chemical perception and load of detoxication enzymes, but not in food utilization efficiencies, between herbivorous insects which are food-plant specialists and those which are food-plant generalists. Ecological advantages can be postulated for herbivorous insects with generalized and for those with specialized feeding habits (such as the ability to better survive in regions with unpredictable and/or physically harsh environments for the former and the potential to store toxic chemicals for protection for the latter) but it is clear that insects exhibiting all categories of phagism continue to exist in nature because of diverse selective pressures.

INTRODUCTION

Interactions between plants and animals are the subject of much current ecological and evolutionary research. One area of interest concerns the degree of specialization of animals feeding on plants. Several studies have mathematically formalized specialization patterns in food selection (e.g. Levins and MacArthur, 1969; Schoener, 1971), and broad patterns of food-plant specialization of animals characteristic of communities in different successional stages have been proposed (Feeny, 1975; Cates and Orians, 1975), but data de-

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¹Present address: Department of Zoology, University of Iowa, Iowa City, Iowa 52242

scribing the patterns actually exhibited by animals have seldom been compiled and analyzed (e.g. Morse, 1971; Scriber, 1973; Cates and Orians, 1975). In this paper the relationships of the major families of Nearctic butterflies to the taxa and growth-forms of their larval food-plants are investigated and compared to those of the Palearctic butterflies (Kostrowicki, 1969). Furthermore, the data are examined in regard to the proposals of Feeny (1975) and Cates and Orians (1975) and a discussion of phagism categories is presented.

METHODS

An extensive survey of the literature was made to determine the genera of the larval food-plants of Nearctic butterflies. Although an attempt was made to exclude erroneous reports (Shields et al., 1969) it is likely that because of the magnitude of this project some errors in food-plant records are included. However, it is felt that these have not influenced to any appreciable extent the results presented. Growth-forms (i.e., tree, shrub, and herb) of the plants in these genera were determined, and the food-plant families were placed in orders following the treatment of Benson (1957). Lists of these data may be obtained from the author upon request. Data for Palearctic butterflies were recalculated from Kostrowicki (1969). The species of butterflies were classed as monophagous if the larvae feed on plants in only one genus and polyphagous if the larvae feed on plants in more than one order. Oligophagous species were defined as those with larvae feeding on plants in more than one genus but only in one order. The oligophagous category was further subdivided into species with larvae feeding on plants in one family and species with larvae feeding on plants in more than one family.

RESULTS AND DISCUSSION

Although the Palearctic butterfly fauna consists of more than three times as many species as the Nearctic fauna, the percentages of the total number of species that the species in each of the families make up are strikingly similar for both the Nearctic and Palearctic butterflies (Table 1). The greatest absolute difference occurs among the Satyridae which contains about 10% of the Nearctic and about 30% of the Palearctic species. Over 90% of all species of both Nearctic and Palearctic butterflies are contained in five families: the Papilionidae, Pieridae, Lycaenidae, Nymphalidae, and Satyridae (Table 1). Of these five main families, the Nearctic Satyridae contains the greatest percentage of species whose larval food-plant genera are not known. A reason for this is that many food-plant 'records' for satyrids merely list 'grasses' and/or 'sedges'. While probably all Nearctic satyrids are restricted to plants in one or both of these two families (Gramineae and Cyperaceae), distinct preferences of the satyrids for various plant genera may occur (Garth & Tilden, 1963) and because of this lack of food-plant records, the following

TABLE 1. Family composition of Nearctic and Palearctic (in parentheses) butterfly faunae and numbers and percentages of species with unknown larval food-plants.

Family	# Species	% Total	Species With Food-Plants Unknown	
			#	%
Nymphalidae	140 (288)	32.4 (21.1)	52 (65)	37.1 (22.6)
Lycaenidae	133 ¹ (375)	30.8 (27.4)	44 (103)	33.1 (24.5)
Pieridae	58 (161)	13.4 (11.8)	15 (35)	25.9 (21.7)
Satyridae	47 (428)	10.9 (31.3)	22 (17)	46.8 (4.0)
Papilionidae	28 (93)	6.5 (6.8)	4 (33)	14.3 (35.5)
Riodinidae	19 (16)	4.4 (1.2)	9 (6)	47.4 (37.5)
Danaidae	5 (6)	1.2 (0.4)	3 (1)	60.0 (16.7)
Libytheidae	2 (1)	0.5 (0.1)	1 (0)	50.0 (0)
Totals	432 (1368)	100.1 (100.1)	150 (260)	34.7 (19.0)

¹ This value does not include *Feniseca tarquinius*, the larvae of which are carnivorous on aphids.

data and discussion deal only with the Papilionidae, Pieridae, Lycaenidae, and Nymphalidae.

That the families of butterflies have similarly diversified in relative numbers of species in both the Nearctic and Palearctic regions indicates similarities among the 'evolutionary success' of the families in the two regions. However, the similar relative diversification has resulted in close similarities among the percentages of polyphagous, oligophagous, and monophagous species only for the Pieridae of each region (Table 2). In terms of the butterflies of these four families as a group, the greatest percentage of species in the Nearctic are monophagous with approximately equal percentages of oligophagous and polyphagous species (Table 2). Shapiro (1973), although using somewhat different criteria¹, likewise found high percentages of monophagous and oligophagous species (about 30–50% in each category) and low percentages of polyphagous species (about 15–20%) in his study of the butterfly fauna of the different regions of New York state. The greatest percentage of species in the Palearctic are oligophagous, followed by a fairly high percentage of polyphagous species and a lower percentage of monophagous species (Table 2).

Various degrees of difference between families and regions occur in the association with plant growth-forms (Table 3). However, the similarities in total percentages for all four families are striking, with herb-feeders predominating in both regions (high percentages of shrub feeders also occur in both regions) (Table 3). If one assumes in a broad sense that the species diversity of herbivorous insects is positively influenced in part by the species

¹ Shapiro included all butterfly families (as well as the HesperIIDae) and he defined oligophagous species as those with larvae feeding on plants in two or more genera in the same family and polyphagous species as those with larvae feeding on plants in two or more families.

TABLE 2. Percentages of species of Nearctic and Palearctic (in parentheses) butterflies in four main families with known larval food-plants that are monophagous, oligophagous, or polyphagous.

Family	# Sp. known	% Known Sp. That Are:		
		Monophagous (1 genus)	Oligophagous	Polyphagous (> 1 order)
Papilionidae	24 (60)	25.0 (25.0)	20.8 (70.0)	54.2 (5.0)
Pieridae	43 (126)	32.6 (30.2)	60.5 (63.5)	7.0 (6.4)
Lycaenidae	89 (272)	55.1 (21.7)	20.2 (44.9)	24.7 (33.5)
Nymphalidae	88 (223)	55.7 (18.4)	13.6 (23.3)	30.7 (58.3)
Totals	244 (681)	48.4 (22.5)	25.0 (43.5)	26.6 (34.1)

diversity of plants, then it would follow that the much greater species diversity of herbs over trees would result in a greater diversity of herb-feeders over tree-feeders. In support of this suggestion is the rather loose yet suggestive correlation between the number of butterfly species and the number of species of vascular plants in the various faunistic regions of the U.S.S.R. (Kostrowicki, 1969).

However, other factors are involved in the determination of insect diversity such that vegetational and herbivorous insect diversities do not necessarily correspond. Southwood (1960; 1961) has found that the number of insect species associated with trees is a function of the evolutionary history of the trees and of their abundance, while Strong (1974) maintains that this variation in insect species richness is explained solely by variations in host tree

TABLE 3. Percentages of species of Nearctic and Palearctic (in parentheses) butterflies in four main families with known larval food-plants that feed on trees, shrubs, and/or herbs.

Family	# Sp. Known	% Known Sp. That Feed On:			Total %
		Trees	Shrubs	Herbs	
Papilionidae	24 (60)	54.2 (30.0)	83.3 (56.7)	54.2 (65.0)	191.7 (151.7)
Pieridae	43 (126)	37.2 (11.9)	44.2 (50.0)	74.4 (72.2)	155.8 (134.1)
Lycaenidae	89 (272)	49.4 (33.8)	70.0 (65.4)	60.0 (67.3)	179.4 (166.5)
Nymphalidae	88 (223)	23.9 (44.0)	51.1 (44.4)	77.3 (54.3)	152.3 (142.7)
Totals	244 (681)	38.5 (32.8)	59.8 (54.9)	68.0 (63.7)	166.3 (151.4)

TABLE 4. Number of species of vascular plants and herbivorous insects and the plant/insect species ratio for various locations in the northern hemisphere.

Place	# Species		Plants
	Vascular Plants	Herbivorous Insects	Insect
New Jersey (40°N)	2,000 ^a	5,200 ^b	0.4
Connecticut (41°N)	2,500 ^c	3,500 ^b	0.7
Britain (50–60°N) ^d	1,600	6,000	0.3
Isachsen (78°N) ^d	50	1	50.0
Lake Hazen (82°N) ^d	100	40	2.5

^a Britton (1889).^b Weiss (1924).^c Graves et al. (1910); Harger et al. (1930).^d Downes (1964).

ranges. Kostrowicki (1969) found no correlation between the number of species of trees, shrubs, and scrubs and the number of species of butterflies feeding on plants with these growth-forms in the various faunistic regions of the U.S.S.R. Among the New World swallowtail butterflies each 'group' associated with different major families of larval food-plants is most diverse (number of species) in the zones where the main larval food-plant families appear most diverse in terms of number of species, but the absolute numbers of swallowtail and plant species do not appear to be directly related (Slansky, 1972). For example, there are in the New World tropics approximately 60 species of swallowtails that feed on plants in the Aristolochiaceae of which there are some 80 species, while in the New World temperate zone there are only about a dozen species of swallowtails that feed on the Umbelliferae of which there are some 250 species. Another example of the lack of correspondence is the relatively greater decrease in insect species over plant species as one proceeds from the north temperate zone towards the Arctic (Table 4).

In as much as several butterflies are recorded as feeding on plants in more than one of the growth-form categories, the total percentages for each family in Table 3 and for each phagism category in Table 5 are greater than 100%. As discussed by Kostrowicki (1969) the degree to which the actual percentages deviate from 100% indicates in an inverse manner how 'attached' species in each of the butterfly families (Table 3) and in each of the phagism categories (Table 5) are to particular plant growth-forms. For example, among the Nearctic butterflies the Papilionidae has the largest total percentage value (Table 3) indicating that the species in this family are the least restricted to particular plant growth-forms.

In regard to the relationship of the phagism categories to growth-forms of the larval food-plants (Table 5), the total percentage values for polyphagous species in each family are greater than the values for monophagous species in each family in both regions (and may or may not be greater than the

TABLE 5. Percentage of the different phagism categories that feed on trees, shrubs, and/or herbs for species of Nearctic and Palearctic (in parentheses) butterflies in four main families with known larval food-plants.

Family	# Sp. Known	% Species That Feed On:			Total
		Trees	Shrubs	Herbs	
Monophagous					
Papilionidae	6 (15)	66.7 (0.0)	83.3 (26.7)	33.3 (93.3)	183.3 (120.0)
Pieridae	14 (38)	64.3 (29.0)	78.6 (84.2)	35.7 (26.3)	178.6 (139.5)
Lycaenidae	49 (59)	44.9 (50.9)	57.1 (59.3)	53.1 (33.9)	155.1 (144.1)
Nymphalidae	49 (41)	12.2 (51.2)	34.7 (53.7)	79.6 (24.4)	126.5 (129.3)
Totals	118 (153)	34.8 (40.5)	51.7 (60.8)	61.0 (35.3)	147.5 (136.6)
Oligophagous					
Papilionidae	5 (42)	40.0 (35.7)	40.0 (64.3)	80.0 (57.1)	160.0 (157.1)
Pieridae	26 (80)	23.1 (2.5)	26.9 (36.3)	92.3 (93.8)	142.3 (132.6)
Lycaenidae	18 (122)	33.3 (19.8)	77.8 (70.5)	77.8 (85.2)	188.9 (175.5)
Nymphalidae	12 (52)	33.3 (51.9)	66.7 (57.7)	100.0 (52.0)	200.0 (161.6)
Totals	61 (296)	29.5 (23.0)	52.5 (58.1)	88.5 (77.4)	170.5 (158.5)
Polyphagous					
Papilionidae	13 (3)	53.9 (100.0)	100.0 (100.0)	53.9 (33.3)	202.8 (233.3)
Pieridae	3 (8)	33.3 (25.0)	33.3 (25.0)	100.0 (75.0)	166.6 (125.0)
Lycaenidae	22 (91)	72.7 (41.8)	90.9 (62.6)	59.1 (64.8)	222.7 (169.2)
Nymphalidae	27 (130)	40.7 (39.2)	74.1 (36.2)	63.0 (65.4)	177.8 (140.8)
Totals	65 (232)	53.9 (40.5)	83.1 (47.0)	61.5 (65.1)	198.5 (152.6)

values for oligophagous species) with the exception of the Pieridae. Thus in the Papilionidae, Lycaenidae, and Nymphalidae, species that are taxonomically polyphagous exhibit a greater degree of overlap in their association with growth-forms of larval food-plants than species that are taxonomically monophagous.

Of considerable interest are the percentages of species that exhibit each type of phagism on plants of each growth-form (Table 6). Feeny (1975)

TABLE 6. Percentage of herb-, shrub-, and tree-feeders in the different phagism categories for species of Nearctic and Palearctic (in parentheses) butterflies in four main families with known larval food-plants.

Family	# Sp. Known	% Species That Are:		
		Monophagous (1 genus)	Oligophagous	Polyphagous (> 1 order)
Herb-Feeders				
Papilionidae	13 (39)	15.4 (35.9)	30.8 (61.5)	53.9 (2.6)
Pieridae	32 (91)	15.6 (11.0)	75.0 (82.4)	9.4 (6.6)
Lycaenidae	53 (183)	49.1 (10.9)	26.4 (56.8)	24.5 (32.2)
Nymphalidae	68 (121)	57.4 (8.3)	17.7 (21.5)	25.0 (70.3)
Totals	166 (434)	43.4 (12.4)	32.5 (52.8)	24.1 (34.8)
Shrub-Feeders				
Papilionidae	20 (34)	25.0 (11.8)	10.0 (79.4)	65.0 (8.8)
Pieridae	19 (63)	57.9 (50.8)	36.8 (46.0)	5.3 (3.2)
Lycaenidae	62 (178)	45.2 (19.7)	22.6 (48.3)	32.3 (32.0)
Nymphalidae	45 (99)	37.8 (22.2)	17.8 (30.3)	44.4 (47.5)
Totals	146 (374)	41.8 (24.9)	21.2 (46.0)	37.0 (29.1)
Tree-Feeders				
Papilionidae	13 (18)	30.8 (0.0)	15.4 (83.3)	53.9 (16.7)
Pieridae	16 (15)	56.3 (73.3)	37.5 (13.3)	6.3 (13.3)
Lycaenidae	44 (92)	50.0 (32.6)	13.6 (26.1)	36.4 (41.3)
Nymphalidae	21 (99)	28.6 (21.2)	19.1 (27.3)	52.4 (51.5)
Totals	94 (224)	43.6 (27.7)	19.2 (30.4)	37.2 (42.0)

has suggested that broad differences may exist in the food-plant relationships of phytophagous insects characteristic of early successional communities and of those characteristic of late successional and climax forest communities, based on the following lines of reasoning: Because of the complexity of many temperate zone early successional communities in terms of the number of plant families represented by species containing different secondary chemicals (e.g. mustard oil glucosides in the Cruciferae, essential oils in the Umbelliferae,

cardiac glycosides in the Asclepiadaceae, alkaloids in the Solanaceae, and cyanogenic glycosides and alkaloids in the Leguminosae), the insects feeding on the plants in these communities are apparently involved in a form of biochemical coevolution that will tend to restrict the number of different plant species used as food. In contrast, because of the lower vegetational diversity of many temperate zone forest communities and because of relatively poor nutritive characteristics (e.g. tough leaves and low water content) and the presence of relatively generalized secondary chemicals (e.g. tannins and resins) in many of the plants, the insects feeding on the plants in these communities are apparently less subject to the restricting form of biochemical coevolution characteristic of the successional herb communities.

Cates and Orians (1975) suggest that early successional plant species, which are apparently selected for rapid growth to escape in 'time' from herbivores and which apparently escape in 'space' as well, would tend to devote less of their energy budget to defense against herbivores than later successional and climax plant species. Consequently, Cates and Orians (1975) predict, contrary to Feeny (1975), that herbivores feeding on early successional plants will tend to be more generalized in their food utilization patterns than herbivores feeding on later successional plants.

If one examines the total percentage values for species in all four families combined (Table 6), one finds some support for the predictions of both Feeny (1975) and Cates and Orians (1975). The high percentages of monophagous and oligophagous herb-feeders in the Nearctic, the high percentage of oligophagous herb-feeders in the Palearctic, and the fairly high percentages of polyphagous tree-feeders in both the Nearctic and Palearctic regions are expected, based on Feeny's (1975) suggestions. The low percentage of monophagous and considerably higher percentage of polyphagous herb-feeders in the Palearctic, and the high percentage of monophagous tree-feeders in the Nearctic support the suggestions of Cates and Orians (1975).

In relation to the polyphagous species, the oligophagous species can be considered as 'specialists' together with the monophagous species. For example, in the Nearctic most of the oligophagous species feed on plants in only one family (Table 7); see also discussion below of the phagism categories. The overall percentages of species in the monophagous and oligophagous categories (Table 6) can thus be combined as 'specialists' and compared to the overall percentages of polyphagous 'generalists' (Table 6) in the light of the proposals being discussed. One now finds that in both the Nearctic and Palearctic regions, the highest percentage of species feeding on each plant growth form are specialized (herb-feeders: Nearctic specialists, 75.9%, and generalists, 24.1%; Palearctic specialists, 65.2%, and generalists, 34.8%. Shrub-feeders: Nearctic specialists, 63.0%, and generalists, 37.0%; Palearctic specialists, 70.9%, and generalists, 29.1%. Tree-feeders: Nearctic specialists,

TABLE 7. Percentage of Nearctic oligophagous species of butterflies in four main families with known larval food-plants that feed on plants in one family or on plants in more than one family in one order.

Family	# Sp. Known	Nearctic Oligophagous Sp.		
		Total %	1 Family	>1 Family
Papilionidae	24	20.8	12.5	8.3
Pieridae	43	60.5	53.5	7.0
Lycaenidae	89	20.2	14.6	5.6
Nymphalidae	88	13.6	11.4	2.3
Totals	244	25.0	20.1	4.9

62.8%, and generalists, 37.2%; Palearctic specialists, 58.1%, and generalists, 42.0%). This indicates that the specializations suggested by Feeny (1975) for herb-feeders and by Cates and Orians (1975) for shrub- and tree-feeders are both prevalent.

Finally, the number of species of shrub-feeders can be combined with the number of species of tree-feeders since shrubs and trees would be expected to exhibit similar herbivore protection strategies (Cates and Orians, 1975), and the calculated percentages of specialized and of generalized shrub- and tree-feeders can be compared to the percentages of specialized and of generalized herb-feeders. In the Nearctic the percentage of specialized herb-feeders (75.9%) is greater than that of specialized shrub- and tree-feeders (62.9%) (Feeny, 1975), while in the Palearctic the respective percentages are very similar (65.2% and 66.1%). Clearly, the situation is complex and only further study can reveal what generalizations, if any, are appropriate. Nonetheless, the fact that a greater percentage of species are specialized than are generalized on all plant growth-forms seems to indicate that specialization, at least among the butterflies studied here, may be more prevalent than expected.

MONOPHAGY, OLIGOPHAGY, AND POLYPHAGY

The distinctions between polyphagous, oligophagous, and monophagous species are of course arbitrary. In the present study, following the categorization of Kostrowicki (1969), monophagous species are defined as those species with larvae feeding on plant species in only one genus. Such species are assumed to be both nutritional and chemical 'specialists', in that the plant species of a genus probably exhibit very similar nutritional and chemical properties. Polyphagous species are here defined as feeding on plants belonging in more than one order. Such species are assumed to be both nutritional and chemical 'generalists' in that the plant species of different orders probably exhibit a great degree of difference in their nutritional and chemical properties. Intermediate between these two categories are the oligophagous species, here defined as feeding on plants in more than one genus but all in one order. The

subdivision of this category for Nearctic butterflies into species that feed on plants in only one family and species that feed on plants in more than one family but restricted to one order (Table 7) reveals that in all four families more species feed on plants in one family than on plants in the different families of an order (the absolute difference is the least for the papilionids where only five species are involved). Thus in relation to polyphagous 'generalists', oligophagous species may be considered as 'specialists' together with the monophagous species.

In spite of this categorization, a certain degree of ambiguity still exists (Painter, 1936). A polyphagous species as defined here may actually be monophagous in terms of the secondary chemistry of the food-plant. For example, larvae of the imported cabbage butterfly, *Pieris rapae*, feed on plants in two separate orders but only on plants containing mustard oil glucosides (Verschaffelt, 1911; Hovanitz et al., 1963). In this regard, Dethier (1947) has suggested that the categories of phagism be divided according to the number of different secondary chemicals used as attractants and/or feeding stimulants by the species. A monophagous species as defined here may actually be a potential oligophagous or polyphagous species. For example, larvae of the West Virginia white, *Pieris virginiensis*, are restricted solely to *Dentaria* plants in the field, reasons for this including habitat selection and synchronization to the phenology of the plants. In the laboratory, however, adults will oviposit and larvae will feed and grow normally on plants in several other genera (Shapiro, 1971; Slansky, 1974). The application of phagism categories in this paper is at the level of the species, but it is clear, for example, that an oligophagous species may or may not be oligophagous at the level of the population and the individual (Neck, 1973; see also Downey & Fuller, 1961; Morse, 1971).

Nonetheless, there are definite distinctions between food-plant 'generalists' and 'specialists'. Fifty years ago Brues (1924) suggested that polyphagous insects might differ from monophagous ones in terms of "more variable instincts," "less restricted powers of digestion," and/or presence of "host races." If 'instinct' is interpreted to mean 'chemical perception' (Brues, 1920), then Brues was correct on this reason. It is now clear that while both generalist and specialist insect species are stimulated to feed by a variety of nutrient compounds (e.g. sugars and amino acids), it is the specialists that usually require the presence of specific secondary chemicals of plants to feed, and it is the specialists that are generally more sensitive to feeding deterrents (Thorpe et al., 1947; Beck, 1956, 1960; Beck & Hanu, 1958; Thorsteinson, 1956, 1958; DeWilde, 1958; Dadd, 1960; David & Gardner, 1966a, 1966b; Moon, 1967; Hsiao & Fraenkel, 1968; Ishikawa et al., 1969; Ma, 1969; Rees, 1969; Dethier & Kuch, 1971; Van Emden, 1972).

Brues' prediction of different digestive abilities between monophagous and

polyphagous insects (Dethier, 1954) appears to fall within the general supposition that a generalist is less efficient in exploiting a particular resource than a specialist for that resource (Morse, 1971). On the basis of rather limited evidence this supposition appears to be incorrect, at least in regard to the physiological food utilization efficiencies of insects. For example, Waldbauer (1964) found that when larvae of the tobacco hornworm, *Protoparce sexta*, which is a specialist insect feeding in nature on plants in the Solanaceae, were maxillectomized so that they would feed on normally rejected plants, the assimilation and growth efficiencies of larvae on some of the plants not normally eaten were almost as high as those exhibited by larvae on the normal food-plants (relative growth rates were however lower), implying that the specialization in this insect has mainly a chemical stimulatory and/or repellant rather than a 'digestive function' basis. SooHoo & Fraenkel (1966) found practically no differences between the assimilation and growth efficiencies of larvae of the generalist southern armyworm, *Prodenia cridania*, and larvae of the specialist silkworm, *Bombyx mori*, when both were fed leaves of white mulberry, *Morus alba* (the usual food of *B. mori*). Likewise, Slansky (1974) found no gross differences in assimilation and growth efficiencies between larvae of the specialist *Pieris virginiensis* and the generalist *P. rapae* when raised on similar food-plants.

A reason for this lack of gross differences in the food-plant utilization efficiencies of generalist and specialist insects is that the nutritional quality of the food-plant is of prime importance in determining the values of the utilization efficiencies (Slansky, 1974; Scriber, 1975), regardless of whether the insect is a specialist or generalist. While there thus appears to be no gross differences in the digestive abilities of specialist and generalist insects, generalist insect species do apparently carry a greater 'load' of detoxication enzymes than most specialist species, apparently because their generalist food habit subjects them to a wider range of potential toxins (Krieger et al., 1971).

Finally, Brues' third prediction regarding the presence of regional and/or seasonal preferences (i.e., Brues' host races) appears fairly well documented for insects of all phagism categories (Brues, 1923, 1946; Buxton, 1923; Brower, 1958a; Downey & Fuller, 1961; Neck, 1973).

Certain advantages associated with generalized and with specialized feeding habits can be postulated (Morse, 1971). For example, a generalized species is less dependent upon the fate of any one plant species and thus would presumably be better able to survive in regions with unpredictable and/or physically harsh environments (Buxton, 1923; Dethier, 1954; Schoener and Janzen, 1968). This supposition is supported by the fact that for the Palearctic butterfly fauna the greatest share of species in arctic and boreal zones are polyphagous (Kostrowicki, 1969), and by the fact that for the

Papilionidae of the world there is a higher percentage of polyphagous species in the temperate zones than in the tropical and subtropical zones (Slansky, 1972; Scriber, 1973). However, the few herbivorous insects found at high altitudes on mountains are primarily monophagous (Mani, 1968). Polyphagy may also allow a species to have a wide geographical distribution (Brues, 1920; Dethier, 1954; Pipkin et al., 1966), although an insect monophagous on a wide-ranging plant can similarly 'benefit' (Brues, 1920). Advantages of specialization, especially upon a generally distasteful plant, include the potential of storing toxic chemicals for protective purposes (Reichstein et al., 1968) and reduction in competition from other herbivores (Reichstein et al., 1968; Rees, 1969), although the specialization need not result from competition for food (Hairston, 1973).

Whatever the advantages and disadvantages of each category of phagism, one cannot conclude that one category of phagism or another is the 'best'. Although specialization is more prevalent than generalization for the butterflies studied here, insects in all categories of phagism continue to exist in nature, and this is clearly the result of diverse selective pressures (Dethier, 1954; Brower, 1958b; Schoener and Janzen, 1968; Levins and MacArthur, 1969; Feeny, 1975).

Literature Cited

- BECK, S. D. 1956. Nutrition of the European corn borer, *Pyrausta nubilalis* (Hbn.). IV. Feeding reactions of first instar larvae. *Ann. Ent. Soc. America* **49**: 399-405.
- . 1960. The European corn borer, *Pyrausta nubilalis* (Hbn.), and its principal host plant. VII. Larval feeding behavior and host plant resistance. *Ann. Ent. Soc. America* **53**: 206-212.
- , AND W. HANU. 1958. Effect of amino acids on feeding behavior of the European corn borer, *Pyrausta nubilalis* (Hbn.). *J. Insect Physiol.* **2**: 85-96.
- BENSON, L. 1957. Plant classification. D. C. Heath and Co., Boston. 688 p.
- BRITTON, N. 1889. Catalogue of plants found in New Jersey. John Murphy Publ. Co., Trenton. 642 p.
- BROWER, L. P. 1958a. Larval foodplant specificity in butterflies of the *Papilio glaucus* group. *Lep. News* **12**: 103-114.
- . 1958b. Bird predation and foodplant specificity in closely related procreptid insects. *American Nat.* **92**: 183-187.
- BRUES, C. T. 1920. The selection of food-plants by insects, with special reference to lepidopterous larvae. *American Nat.* **54**: 313-332.
- . 1923. Choice of food and numerical abundance among insects. *J. Econ. Ent.* **16**: 46-51.
- . 1924. The specificity of food-plants in the evolution of phytophagous insects. *American Nat.* **58**: 127-144.
- . 1946. Insect dietary. Harvard University Press, Cambridge. 466 p.
- BUXTON, P. A. 1923. Animal life in deserts. Edward Arnold and Co., London. 176 p.
- CATES, R. G. AND G. H. ORIAN. 1975. Successional status and the palatability of plants to generalized herbivores. *Ecology* **56**: 410-418.
- DADD, R. H. 1960. Observations on the palatability and utilization of food by locusts,

- with particular reference to the interpretation of performance in growth trials using synthetic diets. Ent. Exp. et Appl. **3**: 283-304.
- DAVID, W. A. L., AND B. O. C. GARDINER. 1966a. The effect of sinigrin on the feeding of *Pieris brassicae* L. larvae transferred from various diets. Ent. Exp. et Appl. **9**: 95-98.
- . 1966b. Mustard oil glucosides as feeding stimulants for *Pieris brassicae* larvae in a semisynthetic diet. Ent. Exp. et Appl. **9**: 247-255.
- DETHIER, V. G. 1947. Chemical insect attractants and repellents. The Blakiston Co., Philadelphia. 289 p.
- . 1954. Evolution of feeding preferences in phytophagous insects. Evolution **8**: 33-54.
- , AND J. H. KUCH. 1971. Electrophysiological studies of gustation in lepidopterous larvae: I. Comparative sensitivity to sugars, amino acids, and glycosides. Z. Vergl. Physiol. **72**: 343-363.
- DEWILDE, J. 1958. Host plant selection in the Colorado beetle larva (*Leptinotarsa decemlineata* Say). Ent. Exp. et Appl. **1**: 14-22.
- DOWNES, J. A. 1964. Arctic insects and their environment. Canadian Ent. **96**: 279-307.
- DOWNEY, J. C., AND W. C. FULLER. 1961. Variation in *Plebejus icarioides* (Lycaenidae). I. Foodplant specificity. J. Lep. Soc. **15**: 34-42.
- FEENY, P. 1975. Biochemical coevolution between plants and their insect herbivores. In L. E. Gilbert and P. H. Raven (Eds.). Coevolution of animals and plants. Symp. 1st Intern. Congr. Syst. & Evol. Biol., Boulder, Colo. Univ. Texas Press, Austin.
- GARTH, J. S., AND J. W. TILDEN. 1963. An ecological survey of the butterflies of the Yosemite section of the Sierra Nevada, California. J. Res. Lep. **2**: 1-96.
- GRAVES, C. B., E. H. EAMES, C. H. BISSELL, L. ANDREWS, E. B. HARGER, AND C. A. WEATHERBY. 1910. Catalogue of the flowering plants and ferns of Connecticut growing without cultivation. State Geol. and Nat. Hist. Sur. Bull. #14. 569 p.
- HAIRSTON, N. G. 1973. Ecology, selection and systematics. Breviora #414. 21 p.
- HARGER, E. B., C. B. GRAVES, E. H. EAMES, C. A. WEATHERBY, R. W. WOODWARD, AND G. H. BARTLETT. 1930. Additions to the flora of Connecticut. State Geol. and Nat. Hist. Sur. Bull. #48. 94 p.
- HOVANITZ, W., V. C. S. CHANG, AND G. HONCH. 1963. The effectiveness of different isothiocyanates on attracting larvae of *Pieris rapae*. J. Res. Lep. **1**: 249-259.
- HSIAO, T. H., AND G. FRAENKEL. 1968. The role of secondary plant substances in the food specificity of the Colorado potato beetle. Ann. Ent. Soc. America **61**: 485-493.
- ISHIKAWA, S., T. HIRAO, AND N. ARAI. 1969. Chemosensory basis of host plant selection in the silkworm. Ent. Exp. et Appl. **12**: 544-554.
- KOSTROWICKI, A. S. 1969. Geography of the Palearctic Papilionoidea (Lepidoptera). Zakład Zool. Syst., Polskiej Akad. Nauk. Panstwowe Wydawnictwo Naukowe. 380 p.
- KRIEGER, R. I., P. P. FEENY, AND C. F. WILKINSON. 1971. Detoxication enzymes in the guts of caterpillars: an evolutionary answer to plant defenses? Science **172**: 579-581.
- LEVINS, R., AND R. MACARTHUR. 1969. An hypothesis to explain the incidence of monophagy. Ecology **50**: 910-911.
- MA, W. C. 1969. Some properties of gustation in the larva of *Pieris brassicae*. Ent. Exp. et Appl. **12**: 584-590.
- MANI, M. S. 1968. Ecology and biogeography of high altitude insects. Dr. W. Junk N. V. Publ., The Hague. 527 p.
- MOON, M. S. 1967. Phagostimulation of a monophagous aphid. Oikos **18**: 96-101.

- MORSE, D. H. 1971. The insectivorous bird as an adaptive strategy. *Ann. Rev. Ecol. and Syst.* **2**: 177-200.
- NECK, R. W. 1973. Foodplant ecology of the butterfly *Chlosyne lacinia* (Geyer) (Nymphalidae). I. Larval foodplants. *J. Lep. Soc.* **27**: 22-33.
- PAINTER, R. H. 1936. The food of insects and its relation to resistance of plants to insect attack. *American Nat.* **70**: 547-566.
- PIPKIN, S. B., R. L. RODRIGUEZ, AND J. LEON. 1966. Plant host specificity among flower-feeding Neotropical *Drosophila* (Diptera: Drosophilidae). *American Nat.* **100**: 135-156.
- REES, C. J. C. 1969. Chemoreceptor specificity associated with choice of feeding site by the beetle, *Chrysolina brunsvicensis* on its foodplant, *Hypericum hirsutum*. *Ent. Exp. et Appl.* **12**: 565-583.
- REICHSTEIN, T., J. VON EUW, J. A. PARSONS, AND M. ROTHSCILD. 1968. Heart poisons in the monarch butterfly. *Science* **161**: 861-866.
- SCHOENER, T. W. 1971. Theory of feeding strategies. *Ann. Rev. Ecol. and Syst.* **2**: 369-404.
- , AND D. H. JANZEN. 1968. Notes on environmental determinants of tropical versus temperate insect size patterns. *American Nat.* **102**: 207-224.
- SCRIBER, J. M. 1973. Latitudinal gradients in larval feeding specialization of the world Papilionidae (Lepidoptera). *Psyche* **80**: 355-373.
- SCRIBER, J. M. 1975. Comparative nutritional ecology of herbivorous insects: generalized and specialized feeding strategies in the Papilionidae and Saturniidae (Lepidoptera). Ph.D. thesis, Cornell Univ., Ithaca, N.Y. 289 p.
- SHAPIRO, A. M. 1971. Occurrence of a latent polyphenism in *Pieris virginiensis* (Lepidoptera: Pieridae). *Ent. News* **82**: 13-16.
- . 1973. Ecological characteristics of the New York state butterfly fauna (Lepidoptera). *J. New York Ent. Soc.* **81**: 201-209.
- SHIELDS, O., J. F. EMMEL, AND D. E. BREEDLOVE. 1969. Butterfly larval food-plant records and a procedure for reporting foodplants. *J. Res. Lepid.* **8**: 21-36.
- SLANSKY, F., JR. 1972. Latitudinal gradients in species diversity of the New World swallowtail butterflies. *J. Res. Lep.* **11**: 201-217.
- . 1974. Energetic and nutritional interactions between larvae of the imported cabbage butterfly, *Pieris rapae* L., and cruciferous food-plants. Ph.D. thesis, Cornell Univ., Ithaca, N.Y. 303 p.
- SOOHOO, C. F., AND G. FRAENKEL. 1966. The consumption, digestion, and utilization of food plants by a polyphagous insect, *Prodenia eridania* (Cramer). *J. Insect. Physiol.* **12**: 711-730.
- SOUTHWOOD, T. R. E. 1960. The abundance of the Hawaiian trees and the number of their associated insect species. *Proc. Hawaiian Ent. Soc.* **17**: 299-303.
- . 1961. The number of species of insects associated with various trees. *J. Animal Ecol.* **30**: 1-8.
- STRONG, D. R., JR. 1974. Nonasymptotic species richness models and the insects of British trees. *Proc. Nat. Acad. Sci. U.S.A.* **71**: 2766-2769.
- THORPE, W. H., A. C. CROMBIE, R. HILL, AND J. H. DARRAGH. 1947. The behavior of wireworms in response to chemical stimulation. *J. Exp. Biol.* **23**: 234-266.
- THORSTEINSON, A. J. 1956. Acceptibility of plants for phytophagous insects. *Proc. 10th Intern. Congr. Ent.* **2**: 599-602.
- . 1958. The chemotactic influence of plant constituents on feeding by phytophagous insects. *Ent. Exp. et Appl.* **1**: 23-27.

- VAN EMDEN, H. F. 1972. Aphids as phytochemists, p. 25-43. *In* J. B. Harborne (Ed.). *Phytochemical ecology*. Academic Press, London.
- VERSCHAFFELT, E. 1911. The cause determining the selection of food in some herbivorous insects. Konink. Akad. Van Wetenschappen te Amsterdam, Proc. Sect. Sci. **13**: 536-542.
- WALDBAUER, G. P. 1964. The consumption, digestion, and utilization of solanaceous and non-solanaceous plants by larvae of the tobacco hornworm, *Protoparce sexta* (Johan.) (Lepidoptera: Sphingidae). Ent. Exp. et Appl. **7**: 253-269.
- WEISS, H. B. 1924. Ratios between the food habits of insects. Ent. News **35**: 362-364.